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Response of *Pheidole morrisi* to Two Species of Enemy Ants, and a General Model of Defense Behavior in *Pheidole* (Hymenoptera: Formicidae)

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ABSTRACT: *Pheidole morrisi* Forel is an omnivorous ant common throughout the eastern United States. Like all members in the genus *Pheidole* the worker force is composed of morphologically distinct soldiers and workers. The aggressive ants *Lasius alienus* (Foerster) and *Solenopsis geminata* (F.) are frequently abundant in the same habitats occupied by *P. morrisi*. Experimental introductions of these two enemy species indicate that Florida colonies of *P. morrisi* alarm-recruit soldiers and workers against *L. alienus* but not against *S. geminata*. These enemy-specific defense responses are compared with defense responses in other *Pheidole* species and a general model of defense behavior is presented.

Recent studies on *Pheidole dentata* Mayr and *Pheidole militicida* Wheeler indicate that the soldier castes, which differ markedly in these two species, are specialized to defend nest sites and food sources against a small subset of potential enemy ant species (Feener, 1981, 1986; Wilson, 1975, 1976a, b). In particular, workers of both these species alarm-recruit soldiers against ants in the genus *Solenopsis* but do not alarm-recruit soldiers against a variety of other ant species. Carlin and Johnson (1984) discovered that the alarm-recruit response of *P. dentata* soldiers against *Solenopsis* is innate, however colonies can also learn to alarm-recruit soldiers against other ant species, including species with no previous contact with *P. dentata*.

The discovery of such enemy-specific defense behavior is of general interest for two reasons. First, it demonstrates that caste division of labor can be unexpectedly specific. Moreover, these studies indicate that morphology and behavior are not necessarily closely associated (Feener, 1986). Second, enemy-specific defense behavior clearly shows that ant colonies not only distinguish between nestmates and alien workers, but also among different species of ants. Differences among species in the expression of this behavior presumably reflect differences in the evolutionary and ecological history of interspecific interactions.

In this paper, I examine the defense behavior of *Pheidole morrisi* Forel against two species of enemy ants, *Lasius alienus* (Foerster) and *Solenopsis geminata* (F.). *P. morrisi* is broadly distributed throughout the eastern United States. It prefers to nest in sandy soil in blow-outs, pastures and open woodlands. The diet of this species consists mostly of insects and other arthropods, and workers occasionally collect seeds. Most of the prey items returned to nests are retrieved by single workers, but nestmates can also effectively cooperate to retrieve prey items that are too large for individual workers.

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L. alienus and *S. geminata* are aggressive species that nest in the same habitat as *P. morrisi*. *L. alienus* is geographically widespread, but is most abundant in the north and central eastern United States (Wilson, 1955). *S. geminata,* in contrast, does not occur in the northeastern United States, but it is abundant in the southeast (Creighton, 1950). The diet of *L. alienus* consists of arthropod prey and honeydew, whereas the diet of *S. geminata* consists of arthropod prey and seeds. Both species employ efficient mass recruitment systems to usurp and defend large or persistent food sources. Where they occur, these species are frequently numerically and aggressively dominant and present a significant competitive threat to other ant species.

Materials and Methods

Field work was conducted between 29 July and 4 August 1983 in open hardwood-pine woodland in the Apalachicola National Forest, 25 km south of Tallahassee, Leon Co., Florida. *P. morrisi* and *S. geminata* were the most abundant soil-nesting species at this locality. Other species present included *Conomyrma* sp., *Pheidole dentata* Mayr, *Pheidole metallescens* Emery and *Pogonomyrmex badius* (Latreille). *L. alienus* did not occur at this locality and, in fact, is rare in northern Florida, the southern limit of its range. I did not find the imported fire ant, *Solenopsis invicta* Buren, in this study site, although it was very abundant in surrounding areas. Presumably *P. morrisi* colonies at this locality had no previous contact with either *L. alienus* or *S. invicta.*

S. geminata workers used in the experiments described below were collected from colonies in the study area. *L. alienus* workers were collected from captive queenless colonies collected in Iroquois Co., Illinois and transported to Florida for the present study. *P. morrisi* was common at this Illinois locality, but *S. geminata* was absent.

Responses of *P. morrisi* colonies to contact with *L. alienus* and *S. geminata* were assessed using the following experimental protocol. Recruitment trails of *P. morrisi* were established by attracting workers to small pieces of tuna fish placed 1.0 m from nest entrances. The number of workers recruited to these tuna baits usually stabilized within 20–30 min. Once recruitment had stabilized, I counted the maximum number of soldiers and workers located within 5 cm of the baits for five successive 1 min periods. After these censuses, I introduced 20 workers of either *L. alienus* or *S. geminata* to the area around the baits and again counted the maximum number of *P. morrisi* soldiers and workers for each of the succeeding 15 min. I collected enemy ants by aspirating them into vials and then introduced them to the area around the baits by placing the vials on their sides and allowing enemy workers to walk out. The collection and introduction procedures did not apparently affect the behavior of either enemy ant species.

Recruitment trails emerging from a total of 12 different colonies were subjected to the experimental procedure described above. In order to minimize learning (Carlin and Johnson, 1984) or other possible carryover effects during the experiments, I introduced each enemy ant species once to each colony. Order of enemy introduction was determined randomly and at least 18 hr separated introductions to each colony.

Results of these experiments were analyzed with a repeated measures analysis of variance (Winer, 1971). The experimental design included enemy and time

main effects (1 and 19 d.f., respectively) and an enemy × time interaction (19 d.f.) repeated across colonies (11 d.f.). Because the primary objective of this study was to determine whether the responses of *P. morrisi* to *L. alienus* and *S. geminata* were different through time, only the enemy × time interaction term was of interest. The correct mean square error term for this interaction term is the mean square for the enemy × time × colony interaction. Significant differences among the means for the enemy × time interaction term were determined by Tukey's Test for Honestly Significant Differences. To ensure that the variances of the enemy × time cells were homogeneous, I used a log transform [log(x + 1)] on soldier and worker counts.

Results

Responses of *P. morrisi* colonies to *Lasius alienus* and *Solenopsis geminata* are shown in Fig. 1. After contact with *Lasius,* both number of soldiers and number of workers at baits increased. Mean number of soldiers changed from 2.7 before introduction to a peak of 5.9 by min 12. Mean number of workers changed from 39 to a peak of 72 by min 13. In contrast to the response against *Lasius,* number of soldiers and number of workers around baits decreased after contact with *Solenopsis.* Mean number of soldiers declined from 1.7 before introduction to 0.7 by the end of the experiment. Mean number of workers fell from 37 to a low of 2.5 by min 8.

Analysis of variance indicates that the responses of *P. morrisi* colonies to *Lasius* and *Solenopsis* as depicted in Fig. 1 were significantly different from one another. The enemy × time interaction is significant for both soldiers ($F[19,209] = 5.565$, $P < 0.001$) and workers ($F[19,209] = 87.597$, $P < 0.001$). A posteriori tests on means indicate that during the 5 min control period the number of soldiers around baits did not differ significantly among treatments. However, after enemy introductions, colonies responded differently. Within 2 min after introduction, there were significantly more workers around baits when *Lasius alienus* was introduced compared to when *Solenopsis geminata* was introduced. These differences were maintained throughout the experimental period. Comparison of means indicated that the same patterns also held for workers, except that responses to enemies were significantly different within a minute after introduction.

Although most colonies responded in a qualitatively similar fashion to the enemies, there was variation among colonies in the intensity of responses. Some colonies responded more strongly to the enemies than others. This heterogeneity among colonies may reflect differences in previous exposure to these enemies (for *Solenopsis* only), variation in colony size or variation in other ecological or genetic variables.

Discussion

This study has demonstrated that Florida colonies of *Pheidole morrisi* respond differently to contact with *Lasius alienus* and *Solenopsis geminata.* When foraging workers of *P. morrisi* contact *L. alienus* they recruit both workers and soldiers. When foragers contact *S. geminata* they flee the area and do not recruit nestmates. Similar enemy-specific alarm-recruitment behavior has been observed in two other *Pheidole* species. The granivorous desert species *Pheidole militicida* preferentially recruits soldiers against *Solenopsis xyloni* McCook but not against the

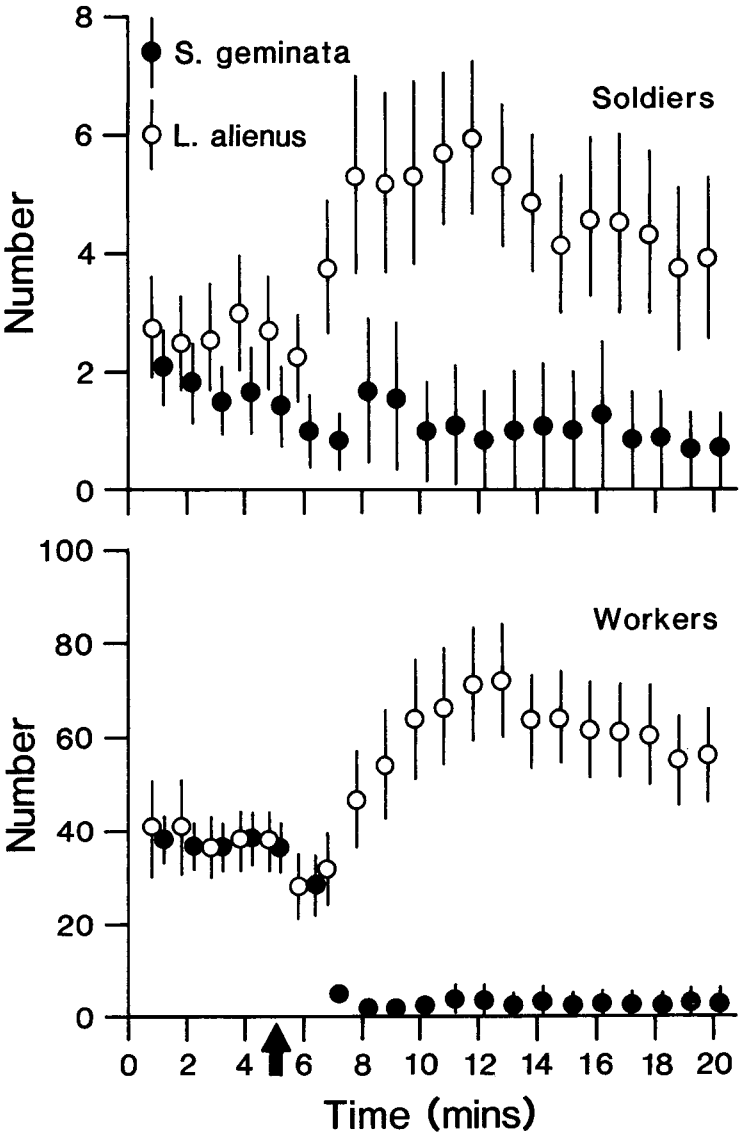

Fig. 1. Recruitment response of *Pheidole morrisi* colonies to introductions of the enemy ants *Lasius alienus* and *Solenopsis geminata*. Open and closed symbols are sample means of 12 replicates. Vertical lines show plus and minus one standard error of the sample means. Means presented here are based on untransformed data. Arrow indicates time of enemy introduction.

seed harvester *Pogonomyrmex maricopa* Wheeler (Feener, 1986). Colonies of *Pheidole dentata,* a species sympatric with *P. morrisi,* also recruit soldiers against at least four species of *Solenopsis* (Feener, 1981; Wilson, 1975, 1976a), but they typically do not recruit them against other ants, including *L. alienus* (Wilson, 1976a). Recently, Carlin and Johnson (1984) demonstrated that laboratory colonies of *P. dentata* can be trained to alarm-recruit against other ant species besides *Solenopsis.* However, *Solenopsis* is apparently the only genus of enemy ant that

evokes an innate alarm-recruitment response from *P. dentata* colonies (Carlin and Johnson, 1984).

Wilson (1976a) found that *P. dentata*'s defense against *S. geminata* is actually a three stage process. If only a small number of *S. geminata* are encountered then foragers recruit soldiers and workers to the contact area. In the field, this area can be several meters from the nest site (Feener, pers. obs.). If a larger number of *S. geminata* are encountered, then foragers abandon the area of contact and soldiers are deployed in a defensive perimeter immediately around the nest. Colonies enter the final phase of defense only if foragers contact an overwhelming number of *S. geminata.* In this case, colonies do not recruit at all, and instead evacuate the nest site and disperse into the surrounding area.

Wilson (1976a) argued that the first stage of enemy-specific alarm-recruitment is an effective defense against more aggressive species if it quickly eliminates small scouting parties and prevents more threatening subsequent recruitment. Because the success of this defense depends on an intense and immediate response, the individuals responsible for this task must be available at a moment's notice and cannot be engaged in other tasks. Consequently, these specialized individuals are usually restricted to the nest until they are needed. In many species of *Pheidole,* soldiers are apparently specialized for this defensive role because their larger heads and more powerful mandibles make them more effective "gladiators" than workers.

Differences in alarm-recruitment responses of morphologically and ecologically similar species such as *P. morrisi* and *P. dentata* are understandable when they are included in a more general framework of colony defense. I suggest that defense behavior in the genus *Pheidole* can be viewed as a four stage process in which there is an increasing threat to the immediate survival of the colony. In the first stage, only generalized workers are enlisted in defense. Fighting typically occurs over food resources away from the nest site and in most cases colony survival is never threatened. Most interactions among mature, well established colonies probably do not escalate past this stage. The other three stages are similar to those found in *P. dentata* (Wilson, 1976a). When a potentially threatening species is first contacted, specialized defenders are alarm-recruited. If the immediate threat to colony survival increases, the colony passes from the alarm-recruitment phase to nest-site defense and finally to nest evacuation.

According to this model, variation among species in response to different enemy ants is due to differences in the threshold number of enemies required to shift from one defense stage to another. Transition thresholds are low for enemy species that frequently threaten colony survival and high for enemies that rarely or never do. These thresholds may be in part genetically determined and in part adjusted to local conditions through behavioral processes such as learning (Carlin and Johnston, 1984).

Differences in responses of *P. morrisi* and *P. dentata* against *S. geminata* and *L. alienus* are consistent with this model of colony defense. Contact with 20 workers of *S. geminata* elicits soldier alarm-recruitment in *P. dentata,* whereas the same number of enemies causes *P. morrisi* foragers to abandon the area of contact. Close inspection of nest entrances of *P. morrisi* indicates that an increase in soldiers just inside the entrances frequently accompanies retreat of the workers. This suggests that the transition threshold from alarm-recruitment to nest site

defense against *S. geminata* is lower in *P. morrisi* than in *P. dentata.* The responses of these two species against *L. alienus* suggest that these thresholds are also lower in *P. morrisi.* The increased sensitivity of *P. morrisi* to *S. geminata* and *L. alienus* may stem from differences in habitat preferences. *P. morrisi, S. geminata* and *L. alienus* all prefer more open habitat than *P. dentata.* Thus, *P. morrisi* probably encounters *S. geminata* and *L. alienus* more frequently than *P. dentata* and this may increase the relative vulnerability of *P. morrisi* to *S. geminata* and *L. alienus.*

This model of colony defense in *Pheidole* also accounts for the observed interspecific variation in response to army ants. *P. dentata* may alarm-recruit soldiers against a small number of army ants, but the response is neither as strong or consistent as its response against *S. geminata* (Wilson, 1976a). In contrast, contact with as few as 5–10 *Neivamyrmex nigrescens* Cresson can provoke nest evacuation in *Pheidole desertorum* Wheeler, *Pheidole hyatti* Emery and *Pheidole subdentata* Pergande (Droual, 1983, 1984; Droual and Topoff, 1981; Feener, pers. obs.). Army ants are far more conspicuous in the southwestern desert and woodland habitats inhibited by these three species than in the southeastern habitats occupied by *P. dentata* and this may indicate differences in the threat to colonies over evolutionary time. If this is so, then it is not surprising that *P. dentata*'s threshold for army ants is higher than in the southwestern species. Other species of *Pheidole* found in the same habitat as *P. desertorum, P. hyatti* and *P. subdentata* do not evacuate nests after contact with a small number of army ants (Mirenda et al., 1980; Feener, pers. obs.). These observations suggest that even within the same habitat, response thresholds may vary among species. Presumably, such variation is due to differences in contact frequency with threatening enemies and species-specific characters related to defense ability such as nest structure and body size of workers and soldiers (LaMon and Topoff, 1981).

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